

**DIPTERA DIVERSITY IN A HOMOGENEOUS HABITAT: BRACHYCERA
ASSOCIATED WITH SEDGE MEADOWS (CYPERACEAE: *CAREX*) IN
QUEBEC, CANADA**

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Abstract.—Species richness and community composition of Brachycera (Diptera) were compared in three sedge meadows dominated by two species of *Carex* (Cyperaceae) in the Lac St. Francois National Wildlife Area in southern Quebec, Canada. More than 10,000 specimens, representing 34 families and more than 338 species, were collected weekly from May to October 1999 by sweeping and yellow pan traps. Species richness was highest in Dolichopodidae, Chloropidae, Sciomyzidae, Syrphidae, Sphaeroceridae, and Ephydriidae. The same families, along with Phoridae, Chamaemyiidae, and Muscidae, were also the most abundant. Overall species composition differed between sites and was apparently influenced by the type of vegetation and substrate. Correspondence analysis showed that habitat associations of the 39 most dominant species differed between sites. The assemblages of Brachycera in the two *Carex lacustris* meadows were similar and richer in saprophagous species than in the *Carex aquatilis* meadow. This is partly due to greater exposure of mud substrate in the *C. lacustris* meadows.

Key Words: Diptera, Brachycera, Nearctic, wetlands, *Carex*, biodiversity, habitat, ecology

Emergent plant communities in wetlands are areas of high biological productivity and conservation significance (Scott 1995, Keiper et al. 2002). The sedge genus *Carex* L. (Cyperaceae) is widespread and diverse in such habitats and is especially dominant in littoral areas, peatlands and wet meadows of temperate regions (Kukkonen and Toivonen 1988).

The aquatic Diptera fauna of temperate wetlands is also species-rich and abundant, mostly due to a few nematoceran families, especially Chironomidae (Wrubleski 1987, Batzer and Wissinger 1996). Fewer studies have examined semi-aquatic or terrestrial Diptera associated with emergent plants or the substrate, although some (e.g., Davis and Gray 1966, Cameron 1972, Pollet

1992, Blades and Marshall 1994, Keiper et al. 2002, Foote 2004) have found high Diptera diversity in marshes and peatlands.

Although their ecological roles are not well-studied, it is increasingly apparent that Diptera are a critical component in food webs and nutrient cycling and are an under-appreciated study group in conservation biology (Haslett 2001, Keiper et al. 2002). Unfortunately, the use of Diptera as model organisms in community ecology and conservation biology is hampered by a lack of baseline knowledge on their diversity and ecology in many habitats, including freshwater wetlands.

Despite the dominance of *Carex* and Diptera in wetlands, there has been relatively little study of their association. Most

ecological studies have focused on selected families such as Chloropidae (Todd and Foote 1987a, Rogers et al. 1991), Ephydriidae (Todd and Foote 1987b) or Scathophagidae (Wallace and Neff 1971) or were in sites where *Carex* was not dominant (e.g., Pollet 1992, 2001). However, Foote (2004) collected 93 species of acalyptrate Diptera associated with *Carex* stands in Ohio and provided notes on abundance, phenology and trophic guilds of selected species. Beaulieu and Wheeler (2001) identified more than 338 species of Brachycera in wetland *Carex* meadows in Quebec, Canada, despite the apparent homogeneity of vegetation and physical structure in that habitat. In this paper, we compare the local species richness and composition of Brachycera in sedge meadows having different physical characteristics and dominated by different *Carex* species.

MATERIALS AND METHODS

Study sites.—The study was conducted in the Lac Saint-François National Wildlife Area (NWA) on the south shore of Lac Saint-François, an enlargement of the St. Lawrence River in southwestern Quebec. The NWA comprises mostly marshes dominated by *Carex* spp. (Cyperaceae) and *Typha* spp. (Typhaceae) and swamps dominated by *Acer rubrum* L. (Aceraceae), *Salix* spp. (Salicaceae), or *Alnus incana* (L.) Moench. (Betulaceae) (de Repentigny and Fragnier 1986, Jean and Bouchard 1991). Three sample sites were chosen on the basis of dominance and homogeneity of *Carex*. All sites were open habitats with a herbaceous layer between 1.05–1.10 m in height. Trees were present only on the periphery. Sites LAC1 (45°00.39'N, 74°30.99'W) and LAC2 (45°00.17'N, 74°30.63'W) were about 1 km apart; site AQU1 (45°02.40'N, 74°28.03'W) was about 11 km from the others. Beaulieu and Wheeler (2001) listed the plant species recorded at each site.

Site AQU1 (F1 in Beaulieu and Wheeler 2001) was about 0.16 ha in size and was dominated by *Carex aquatilis* Wahlenb. and

Calamagrostis canadensis (Michx.) P. Beauv. (Poaceae). *Carex lacustris* Willd. was abundant, but less so than at the other sites. Plant diversity and overall heterogeneity were higher at AQU1 than at the other sites. The substrate consisted of hollows of firm wet soil interspersed with tussocks of sedges and other vegetation. From late April until late May the water depth was 0–15 cm; for most of the summer the water table was near the surface and the soil was moist to saturated. The water depth increased to 5 cm in mid October and the site remained covered by water for the rest of the season. The surrounding area was dominated by *C. lacustris*, *C. aquatilis* and *A. incana*.

Site LAC1 (T1 in Beaulieu and Wheeler 2001) was about 0.12 ha in size with an almost pure stand of *C. lacustris*, at a density of 277 ± 14.8 stems/m² (mean \pm SD based on multiple 1 m² quadrats) in mid July. The substrate was homogeneous, flat and muddy. The water level was similar to that at AQU1 before and during the sampling period, with a gradual increase in water depth from 0–5 cm to 15–25 cm from mid September until late October. The vegetation of the surrounding area was more diverse.

Site LAC2 (T2 in Beaulieu and Wheeler 2001) was about 0.17 ha in size with an almost pure stand of *C. lacustris*, at a density of 166 ± 14.8 stems/m². The substrate was similar to LAC1, although the exposed mud was more extensive because of the lower density of *Carex*. There were more puddles of standing water than at LAC1 and water depth increased from about 0 cm during most of the sampling period to 0–5 cm in mid-September and 10–20 cm in mid-October. The surrounding area contained a variety of herbaceous plants, although *C. lacustris* was still dominant.

Specimen collection and preparation.—Flies were collected every 6–8 days from 14 May to 27 October 1999. Four yellow pan traps (15 cm diameter, 4 cm deep) were placed in a 5 m square in the center of each

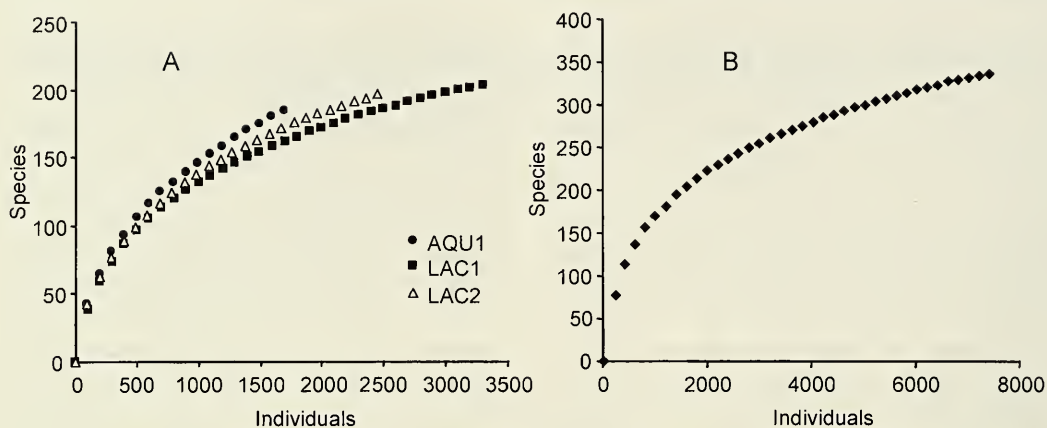


Fig. 1. Rarefaction (collector's) curves for *Brachycera* species collected in each study site (A) and all sites pooled (B).

site. Traps were set with their upper rim flush with the ground surface in sites where the water had receded; traps were filled with propylene glycol, and a drop of liquid detergent was used as a wetting agent. Vegetation was also swept at mid-day using a 37.5 cm aerial net for 20 sweeps along each of three random 20 m transects at each site. The location of transects within each site differed from week to week.

Insects were preserved in 70% ethanol. Small flies were dried using hexamethyldisilazane; large flies were pinned and then transferred to ethyl acetate for 24h before air-drying. All specimens were deposited in the Lyman Entomological Museum, McGill University, Ste-Anne-de-Bellevue, QC.

Most specimens were identified to named species (where possible) or morphospecies; Anthomyiidae, Fanniidae, and most Phoridae were not sorted to species. In all analyses, morphospecies were treated as equivalent to named species; unsorted genera were not included except for the calculation of the number of individuals per trophic group, where feeding behavior in the genus could be inferred.

Data analysis.—Species richness was calculated based on all species collected at each site over the season. Data from pan traps and sweeping were combined in all analyses except in some correspondence

analyses. To examine sampling efficiency in measuring species richness, rarefaction or collector's curves were plotted using the program *EstimateS* version 6 (Colwell 2000), with 40 randomizations for each curve. Non-parametric estimators of species richness (ACE, Chao1, Jack1) were calculated using *EstimateS*.

Species composition among sites was compared using the Jaccard index, which is based on presence-absence of species, and the Bray-Curtis coefficient, which incorporates species abundance (Legendre and Legendre 1998). To minimize the influence of accidental visitors, species represented by a single specimen at a site were omitted from that site in calculating the indices and the number of species shared between sites (Table 3), reducing the number of species included in the analyses from 338 to 234. Both indices were calculated for all species pooled and for the six dominant families individually.

Species composition within and among sites was also compared using correspondence analysis (CA). Replicates of pan traps were used in the analysis but data were pooled for all three sweep samples in each site (within-site replicates were not considered because sweep samples were not taken along the same transects each week). The CA was conducted using the program

Table 1. Number of species and specimens of dominant (ten species) families of Brachycera.

Family	Species				Specimens			
	AQU1	LAC1	LAC2	Total	AQU1	LAC1	LAC2	Total
Dolichopodidae ¹	26	23	30	49	184	192	282	658
Chloropidae	34	26	20	45	398	1,133	273	1,804
Sciomyzidae	16	25	22	31	106	279	277	662
Ephydriidae	8	19	25	31	19	110	186	315
Syrphidae	12	17	12	25	110	116	107	333
Sphaeroceridae ¹	12	15	18	22	187	571	627	1,385
Muscidae	8	9	14	21	144	150	135	429
Empididae	12	11	10	18	34	38	66	138
Agromyzidae	7	6	1	11	21	13	9	43
Tabanidae	5	9	8	10	18	36	31	85
Scathophagidae	5	6	4	10	15	8	11	34
All Brachycera	184	203	196	338	2,825	4,045	3,519	10,384

¹ *Chrysotus* Meigen (Dolichopodidae) and *Leptocera* Olivier (Sphaeroceridae) are included in specimen totals but not species totals.

SAS version 6.12 (SAS Institute 1996). Pan trap samples were ordinated according to their similarity in relative abundance of species and were then projected on the two axes that explained the largest amount of variation in species abundance among samples. One CA was conducted for pan traps and a second for sweep samples. Only species represented by more than ten specimens (51 species in total, for both CA) were included in the analysis to minimize the influence of rare species. Prior to CA, numbers of specimens were transformed into percentages of the total abundance of the species over all sites. A third CA was conducted using only the 39 most dominant species (those represented by at least 30 specimens). Both sampling methods were pooled in this analysis and the three study sites were plotted on the same axes. The dominant species were then plotted on the same graph to show their distribution among the sites.

RESULTS

Species richness and abundance.—Although 338 species were identified, most were collected in low numbers; 31.5% of species were singletons and 11.6% were represented by only two specimens (see Beaulieu and Wheeler (2001) for a com-

plete species list with number of specimens collected, comparison of pan traps versus sweeping, and trophic groups).

Species richness was similar in all sites, with 184 to 203 species each (Table 1). ACE, Chao1 and Jack1 all estimated a minimum of 260 species at each site (Fig. 1a), suggesting that about 25% of species actually present were not collected. For all sites pooled, the rarefaction curve (Fig. 1b) did not reach an asymptote, and ACE, Chao1 and Jack1 estimated that at least 434 species may be present.

Species richness was highest in early to mid June, especially in LAC1 and LAC2 where 64–80 species were collected per week (Fig. 2c) but at least 15 species per week were collected until late October. Sciomyzidae, Sphaeroceridae and Ephydriidae were largely responsible for the higher species richness in LAC sites in May and June (Fig. 2).

Dolichopodidae, Chloropidae, Sciomyzidae, Ephydriidae, Syrphidae, and Sphaeroceridae were the most species-rich families in all sites (except that Ephydriidae were less speciose in AQU1 and Muscidae exceeded Syrphidae in LAC2) (Table 1). These six families contributed $62.3 \pm 2.8\%$ (mean \pm SD) of all species at each site. The same families were also dominant in num-

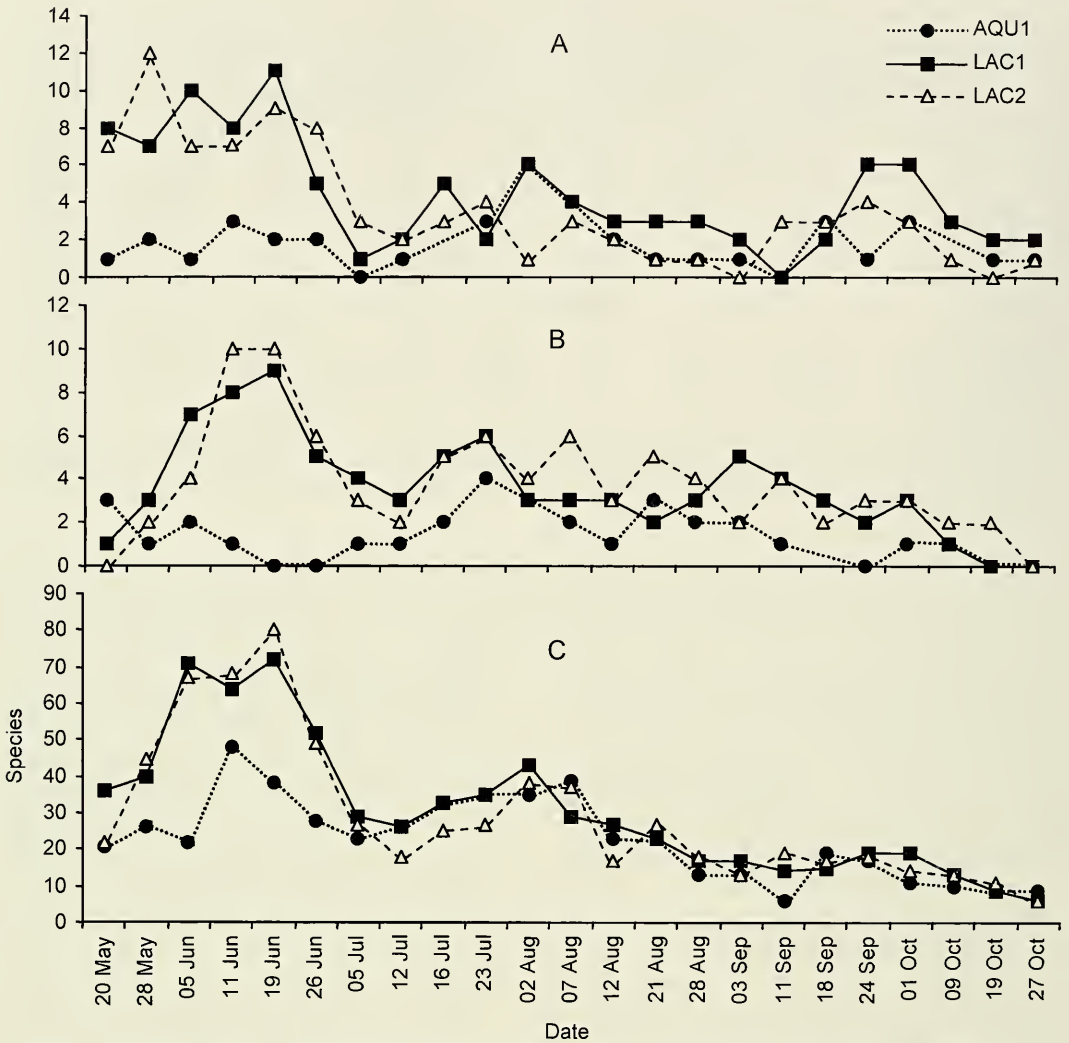


Fig. 2. Seasonal pattern of species richness in Sciomyzidae (A), Sphaeroceridae (B), all Brachycera (C) (excluding Phoridae, Anthomyiidae and *Chrysotus* (Dolichopodidae)). No pan traps were installed in site LAC2 during the first sampling week.

bers of individuals (except Ephyridae in AQU1) (Table 1). Chamaemyiidae, Phoridae, and Muscidae were also collected in high numbers at all sites (1990, 1654, 427 specimens, respectively). The dominance of Chamaemyiidae was primarily due to *Plunomia elegans*, which accounted for 18.5% of all flies collected.

Comparison of species composition between sites.—Only 73 species (21.6%) were collected at all three sites; 37 of those were represented by at least ten specimens.

Chloropidae, Dolichopodidae, and Sciomyzidae were a major component of this widespread set of species.

LAC1 and LAC2 shared 28 species represented by at least ten individuals, and 57 species overall. Sciomyzidae, Ephyridae and Sphaeroceridae were a major component of the assemblage collected only in LAC sites; all three were more speciose and abundant in LAC sites than in AQU1 (Table 1). These families also contributed to the higher Jaccard and Bray-Curtis coefficients

between LAC sites (all families, Table 3), than between either LAC site and AQU1. AQU1 shared only eight species with more than 10 individuals (23 species overall) with LAC1, and four species with more than 10 individuals and 17 species overall with LAC2.

Few of the dominant species were unique to a single site; most species collected at a single site were represented by very few specimens. Eleven species represented by at least ten individuals, and 70 species in total, were unique to AQU1, compared to three dominant species (50 in total) unique to LAC1 and two dominant species (49 in total) in LAC2.

The four pan traps in each site clustered together in the CA of pan trap samples (Fig. 3, inset), indicating that variation in species abundance within each site was lower than that among sites. The first and second axes explained 45.1% and 13.1% of the total variance, respectively. Two axes explained 100% of the variance for sweeping because only three samples were included. In both analyses, the species assemblages in LAC sites were more similar to each other than to AQU1.

Habitat associations of dominant species.—In the CA of dominant species (Table 2), two axes explained 100% of the variation in species abundance among sites because only three sites were compared (Fig. 3). Dominant species were divided into three groups. Group I species (triangles, Fig. 3) were collected exclusively or primarily in LAC1 and/or LAC2. This was the largest group, with 22 (56.4%) species. Twelve species were assigned to Group II (circles, Fig. 3), abundant in all three sites. Five species were assigned to Group III (squares, Fig. 3), collected exclusively or primarily in AQU1. *Plunomia elegans* was by far the most abundant species at all sites; comments on selected families represented by multiple dominant species follow.

Twelve of the dominant species (30.8%) were Chloropidae; larvae of most of these are saprophagous secondary invaders.

Three species, *Rhopalopteron soror*, *R. n. sp. nr soror* and the phytophagous species *Pseudopachychaeta approximatonervis* were entirely or mostly associated with AQU1. *Rhopalopteron atriceps* and *Incertella bispina* were more abundant in AQU1, whereas *Incertella n. sp. 1* was more abundant in LAC1. *Eribolus longulus*, *Elachiptera nigriceps*, *E. pechumani*, and *E. penita* were primarily associated with LAC sites. *Chlorops seminiger* (phytophagous) and *Dasyopa n. sp. 1* (larval habits unknown) were more abundant in LAC sites.

Five of the seven dominant Sciomyzidae (*Elgiva sollicita*, *Pherbellia vitalis*, *P. anubis*, *Sepedon spinipes americana* and *Tetanocera ferruginea*) were associated with LAC sites. The two other dominant species, *Dictya steyskali* and *Poecilographa decora*, were among the few mainly associated with AQU1.

Three dominant species of Sphaeroceridae (*Phthitia quadricercus*, *Rachispoda n. sp. 1*, *Rudolfina n. sp. 1*) were almost entirely confined to LAC sites. *Pullimosina pullula* was most abundant in LAC sites, but was also collected in AQU1.

Dolichopodidae, Syrphidae, and Muscidae had three dominant species each. In all cases those species were either abundant in all sites (six species) or entirely or mostly restricted to LAC sites.

Diversity and abundance of trophic groups.—The trophic group or subgroup (Table 4) was known for some species and was inferred for other species from published records on congeners. The trophic group was tentative for ten species and unknown for 24 species. Many species, especially saprophages, were not assigned to a trophic subgroup, either because they have been reared from a range of decaying media or because their exact food source is unknown. As a result, total species numbers for trophic groups do not always correspond to the sum of species assigned to trophic subgroups (Table 4).

Predators and saprophages were the most species-rich (145 and 118 species, respec-

Table 2. Number of specimens (n), frequency of collection (f) and larval trophic group (Trph) of dominant species. Species codes used in Fig. 4 precede species name.

Code	Species	Family ¹	AQU1			LAC1			LAC2			Trph ³
			n	f	n	f	n	f	n	f		
Pele	<i>Plutonium elegans</i> Curran	CHA	468	+++	770	+++	682	+++			PRap	
Incl	<i>Incertella</i> n. sp. 1	CHL	114	++	587	+++	44	+			SAsi	
Elon	<i>Eribolus longulus</i> (Lw.)	CHL	18	++	232	+++	49	+++			SAsi	
Ncau	<i>Notiphila caudata</i> Fall.	EPH	7	+	63	+++	121	+++			SAsu	
Cmas	<i>Chaetopsis nasyyla</i> (Walker)	OTI	22	+++	76	+++	69	+++			SAsi	
Pvit	<i>Pherbellia vitalis</i> (Cresson)	SCI	1	-	56	++	98	++			PRmo	
Cery	<i>Caricea erythropera</i> R.-D.	MUS	78	+++	50	++	26	++			PR	
Das1	<i>Dasyopa</i> n. sp. 1	CHL	1	-	97	++	39	+			?	
Nmet	<i>Neosacia metallica</i> (Williston)	SYR	65	++	29	++	49	+++			?	
Pqua	<i>Phititia quadricercus</i> Marshall	SPH	1	-	33	+++	94	+++			SA	
Prud	<i>Pollenia rudis</i> Fabr.	CAL			65	+++	63	+++			PA	
Maus	<i>Macrorchis ausoba</i> (Walker)	MUS	28	++	43	++	56	+++			?	
Ppul	<i>Phlimosina pullula</i> (Zett.)	SPH	12	++	61	+++	46	+++			SA	
Eng	<i>Elachiptera nigriceps</i> (Lw.)	CHL	5	-	17	+	65	++			SAsi	
Grap	<i>Graphomyia</i> sp. 1	MUS	3	+	47	++	34	++			PRsu	
Ibis	<i>Incertella ?hispinga</i> (Malloch)	CHL	51	++	26	+	6	+			SAsi	
Dalb	<i>Dolichopus albiciliatus</i> Lw.	DOL	10	+	25	++	47	+			PRsu	
Esol	<i>Elgiva sollicita</i> (Harris)	SCI	6	++	42	+++	29	+++			PRmo	
Gpur	<i>Gymnopternus purpuratus</i> (Van Duzee)	DOL	19	+	41	+	15	+			PRsu	
Sarc	<i>Sarcotachinella sinuata</i> (Mg.)	SAR	25	++	25	++	22	+			PA	
Tfer	<i>Tetanocera ferruginea</i> Fall.	SCI			30	++	41	++			PRmo	
Rae1	<i>Rachispoda</i> n. sp. 1	SPH	41	++	29	+++	41	++			SAsu	
Ratr	<i>Rhopalopterum atriceps</i> (Lw.)	CHL			19	+	2	-			SAsi	
Llin	<i>Lejops lineatus</i> (Fabr.)	SYR	12	+	29	+	12	++			SAsu	
Plac	<i>Parhelophilus laetus</i> (Lw.)	SYR	3	-	24	+	20	+			SAsu	
Pdec	<i>Poecilographa decora</i> (Lw.)	SCI	46	++							PRmo	
Phol	<i>Platypalpus holosericus</i> Melander	EMP			6	+	39	+			PRsu	
Epen	<i>Elachiptera penita</i> (Adams)	CHL	2	-	22	++	17	++			SAsi	
Epec	<i>Elachiptera pectunani</i> Sabrosky	CHL	2	-	30	++	7	+			SAsi	
Sspi	<i>Sepedon spinipes americana</i> Steyskal	SCI	2	-	14	++	23	+			PRmo	
Panu	<i>Pherbellia anubis</i> Knutson	SCI	2	-	13	+	21	++			PRmo	
Csem	<i>Chlorops semiinger</i> Becker	CHL	4	-	20	+	11	+			PHsb	
Rudo	<i>Rudolfina</i> n. sp. 1	SPH			11	++	24	+++			SA	

Table 2. Continued.

Code	Species	Family ¹	AQU1		LAC1		LAC2		Trph ³
			n	f	n	f	n	f	
Papp	<i>Pseudopachychaeta approximatonervis</i> (Zett.)	CHL	23	++	6	+	4	+	PHfl
Bsil	<i>Bifolucilia silvarum</i> (Mg.)	CAL	1	-	11	++	21	++	SA
Dste	<i>Dictya steyskali</i> Valley	SCI	26	++	5	+	1	-	PRmo
Rsor	<i>Rhopalopterum soror</i> (Macq.)	CHL	28	+	2	-	1	-	SAsi
Came	<i>Campsicnemis americanus</i> Van Duzee	DOL							PRsu
Rnsu	<i>Rhopalopterum</i> n. sp. nr. <i>soror</i>	CHL	30	+			31	++	SAsi

¹ Family: CAL = Calliphoridae; CHA = Chamaemyiidae; CHL = Chloropidae; DOL = Dolichopodidae; EMP = Empididae; EPH = Ephydriidae; MUS = Muscidae; OTI = Otitidae; SAR = Sarcophagidae; SCI = Sciomyzidae; SPH = Sphaeroceridae; SYR = Syrphidae.

² Proportion of sampling dates on which species was collected; - = 1-10%; + = 11-25%; ++ = 26-50%; +++ = over 50%.

³ PA = parasitoid; PH = phytophage (sb = in stems; fl = in flowerhead); PR = predator (ap = on aphidoids; mo = on molluscs; su = in substrate); SA = saprophage (si = secondary invader; su = in substrate); ? = unknown.

tively) and abundant (3,862 and 5,411 individuals) groups, each representing over one third of all species and specimens (Table 4). The aphidophagous *Plunomia elegans* accounted for half of the predaceous flies (1920 specimens). Although there were 33 phytophagous species, they were not abundant. There were few parasitoids or omnivores. AQU1 had fewer saprophagous species, particularly those living in the substrate, and the highest number of phytophagous species. There were fewer phytophagous species in LAC2. Secondary invaders were particularly abundant in LAC1, mainly because of two chloropids, *Incertella* n. sp. 1 and *Eribolus longulus*. Gastropod predators were more abundant and diverse in LAC1 and LAC2 than in AQU1.

DISCUSSION

Diversity of Brachycera.—Brachycera are a dominant component of the insect community in sedge meadows. Unlike many wetlands, our sites were only temporarily flooded, with almost no standing water during most of the summer; this seasonal difference in water level may be an important factor regulating the Brachycera fauna. Emergent plants such as *Carex* and a mud substrate offer suitable breeding sites for phytophagous species, secondary invaders, detritivores and predators associated with plants and wet soil. The homogeneous habitat in the *C. lacustris* sites, composed almost exclusively of one plant species and a uniform substrate, supported more species than the *C. aquatilis* site, in which the flora and substrate were more heterogeneous. The greater diversity of Brachycera in pan traps in LAC sites was probably related to the mud substrate. Many fly larvae develop in mud (Irwin 1978), and the substrate of emergent marshes like the LAC sites could support large populations of detritivores or microbial grazers (e.g., ephydrids, sphaerocerids, syrphids) and semi-aquatic predators (e.g., dolichopodid larvae). These families were more abundant in LAC sites and some (e.g., dolichopodids, ephydrids,

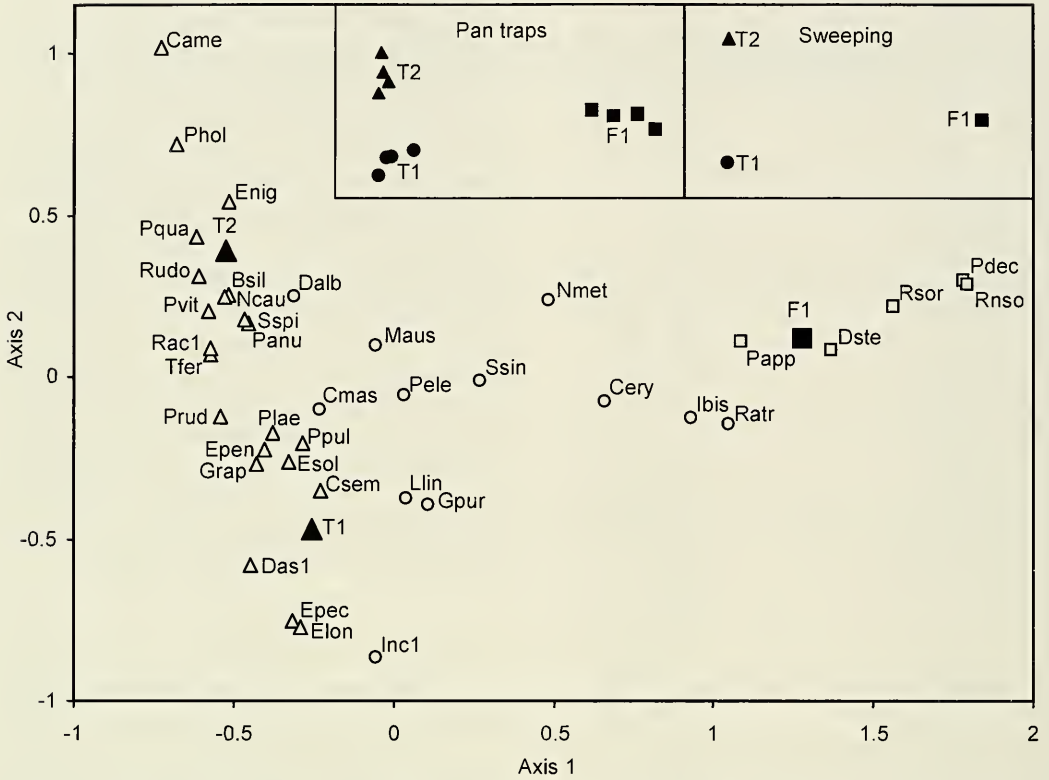


Fig. 3. Correspondence analysis ordination of study sites (insets) and dominant Brachycera species. Shaded symbols = study sites; open triangles = Group I species; open circles = Group II species; open squares = Group III species.

sphaerocerids) were most abundant in LAC2 where there was more moisture and exposed mud.

According to the estimates of species richness, many species presumably present in the sites during the sampling period were not collected. Comparison of the species

collected in LAC1 and LAC2 supports this; the two sites were within 1km of one another and represent basically the same habitat but many species were collected in only one of the sites. Many of these species may have been “tourists” whose presence was due to conditions in the surrounding habi-

Table 3. Similarity in species composition (excluding singletons) between pairs of sites for six most dominant families and all Brachycera. JAC = Jaccard index, B-C = Bray-Curtis coefficient, shared = number of species shared.

Family	LAC1/LAC2			AQU1/LAC1			AQU1/LAC2		
	Jac	B-C	Shared	Jac	B-C	Shared	Jac	B-C	Shared
Dolichopodidae	0.48	0.51	10	0.35	0.40	7	0.25	0.31	6
Chloropidae	0.52	0.30	13	0.41	0.28	13	0.44	0.30	12
Sciomyzidae	0.67	0.68	16	0.32	0.18	8	0.29	0.12	6
Ephydriidae	0.44	0.63	8	0.40	0.25	4	0.18	0.16	3
Syrphidae	0.40	0.67	4	0.60	0.49	6	0.56	0.68	5
Sphaeroceridae	0.56	0.66	10	0.20	0.23	3	0.13	0.15	2
All Brachycera	0.51	0.64	92	0.30	0.41	57	0.27	0.43	51

tats, such as phytophagous species in families like Agromyzidae or Tephritidae whose host plants were present near the sample sites. Such accidental visitors should not be considered equivalent to truly rare inhabitants of the site, but given the lack of information on ecology of many species, it is often difficult to discriminate between true inhabitants and tourists that were simply carried by wind (often substantial in open shoreline habitats). An additional confounding factor is that some species may not inhabit sedge meadows throughout their larval stages but may use them solely for adult resting, feeding or mating sites (Delettre et al. 1998). Additional inventories carried out in a range of habitats (e.g., marshes, swamps, meadows) as well as ecological studies of larval habits and habitats may help to resolve the status of resident species, transient species who use the habitat during part of their life cycle and true "tourists."

Habitat associations of dominant species.—The habits and habitats of many Brachycera species are unknown; this is an obstacle to ecological research on the group. Some taxa have been studied in detail, ecological data are also scattered in taxonomic publications and inferences about some species can be made by comparison with observations on related species. Although it is difficult to establish habitat associations based on only three sites representing two similar habitats, some general patterns were noted in some dominant families and species.

Dolichopodidae are diverse and abundant predators in wet habitats such as marshes and peatlands (Pollet 1992, 2001; Blades and Marshall 1994). Although most of our 49 species were collected in low numbers, *Carex* meadows are clearly a suitable habitat. The fact that 18 species were represented by singletons suggests either that additional rare species have been missed or that adults of many species range widely in search of prey.

Some Syrphidae may be closely associ-

ated with *Carex* and mud substrates. Maibach and de Tiefenau (1993) studied larvae of four European species of *Neoscia* Williston and found one exclusively between leaves of *Typha*, one between leaves of *Carex*, one in soil or among mosses, and the fourth in a variety of habitats including *Carex* and organic soils. Thus, *N. metallica* may develop in *Carex* stems and/or wet mud. It is not known whether all species of the genus are predaceous or saprophagous. Larvae of *Lejops* Rondani and *Parhelophilus* Girschner breed in mud, probably feeding on detritus and microorganisms like many other Eristalini (Ferrar 1987). Blades and Marshall (1994) collected *Lejops* and *Neoscia* species in Ontario fens and bogs. Five species of *Platycheirus* Lepeletier and Serville identified in this study have been previously collected in *Carex* marshes (Vockeroth 1992), although there is no other habitat information on those species.

Sciomyzidae thrive in wetlands and their abundance in all study sites suggests that suitable host snails are abundant. The five dominant species (*Elgiva sollicita*, *Pherbellia vitalis*, *P. anubis*, *Sepedon spinipes americana* and *Tetanocera ferruginea*) in LAC sites feed on a variety of aquatic pulmonate snails. Knutson and Berg (1964) recorded adults of *E. sollicita* in emergent herbaceous vegetation of marshes, ponds, lake margins, and stream banks. Bratt et al. (1969) found *P. vitalis* and *P. anubis* dominant in vernal marshes where the water recedes during summer, exposing snails on the mud or vegetation. *Pherbellia anubis* apparently prefers partially shaded *Carex* marshes but *P. vitalis* has been collected in a range of habitats from swamps to tundra. Adults of *S. spinipes americana* are found on low vegetation in marshes, wet meadows and fens (Neff and Berg 1966, Blades and Marshall 1994). Larvae of *T. ferruginea* have been collected in shallow water among aquatic macrophytes (Foote 1999). The habits of *Dictya steyskali*, dominant in AQU1, are unknown but other *Dictya* spp. are found in a variety of habitats such as

Table 4. Brachycera species and species and specimens (in parentheses) by larval trophic group or subgroup. Subgroup totals do not always add up to group total (see text).

Trophic Group [or subgroup]	Site			Total
	AQU1	LAC1	LAC2	
Phytophagous	23 (99)	17 (60)	9 (36)	33 (195)
[Stem-borer]	11 (46)	5 (25)	4 (20)	12 (91)
[Leaf-miner]	7 (19)	7 (14)	2 (10)	13 (43)
[Flowerhead feeder]	5 (34)	3 (8)	2 (5)	6 (47)
Saprophagous	55 (1,491)	80 (2,164)	79 (1,756)	118 (5,411)
[Secondary invader]	17 (334)	19 (1,070)	14 (280)	24 (1,684)
[In substrate]	16 (50)	32 (240)	37 (293)	49 (583)
Predaceous	78 (1,004)	79 (1,427)	87 (1,431)	145 (3,862)
[Aphidoid predator]	13 (552)	9 (790)	8 (706)	22 (2,048)
[Mollusc predator]	16 (106)	25 (279)	22 (277)	31 (662)
[In substrate]	43 (230)	40 (256)	48 (376)	76 (862)
Parasitoid	6 (40)	8 (113)	7 (100)	13 (253)
Omnivore	2 (5)	3 (5)	1 (2)	3 (12)
Unknown	13 (143)	14 (234)	11 (163)	24 (540)

marshes, wet woodland, wet meadows and bogs (Valley and Berg 1977). The larval habits of *Poecilographa decora* are unknown, but adults are associated with wetlands and puparia have been collected in a bog and a wooded swamp (Barnes 1998).

Chloropidae are dominant in wetlands and many species feed on monocots (Ferrari 1987, Beaulieu and Wheeler 2002). They were one of the most species-rich families in this study, particularly in AQU1, where monocot diversity was higher. Some phytophagous species, such as *Meromyza flavipalpis* Malloch (stem-borer in grasses) and *Dicraeus fennicus* Duda (flowerhead feeder in grasses), were collected only in AQU1. *Chlorops seminiger* was dominant in LAC sites and has been reared from *C. lacustris* (Beaulieu and Wheeler 2002). *Pseudopachychaeta approximatonervis* has been reared from flowerheads of *Eleocharis* R. Br. (Cyperaceae) (Valley et al. 1969, Todd and Foote 1987a) and *Scirpus* (B.A. Foote, personal communication), but these hosts were absent in and near AQU1 and this species may also feed in *Carex*.

Secondary invaders comprised about half of the chloropid species (including most of the dominant species) and over two-thirds of the specimens collected. *Eribolus lon-*

gulus is associated with sedges and grasses in wet habitats (Valley et al. 1969, Beaulieu and Wheeler 2002). *Elachiptera pechumani* has been reared from *Iris* spp. (Valley et al. 1969) and *E. penita* from *Phalaris arundinacea* L. (Poaceae) (Beaulieu and Wheeler 2002), but their abundance in LAC sites and the rarity of known host plants in the area suggest that *C. lacustris* is also a host. *Rhopalopterum atriceps* has been reared from *Carex comosa* F. Boott. and *C. lacustris* (Valley et al. 1969, Beaulieu and Wheeler 2002) and its abundance in AQU1 suggests that *C. aquatilis* is also a host. The dominance of *Incertella* n. sp. 1 in all sites suggests that it is a secondary invader of *Carex*.

Several species of Sphaeroceridae collected in our study are also found in peatlands, and Marshall (1994) considered three of those (*Phthitia quadricercus*, *P. ovicerus* Marshall, *Spelobia pappi* Roháček) characteristic of that habitat. Our sites share some characteristics with peatlands (wet organic soil, presence of *Carex*). *Phthitia* spp. are usually found in wet plant material (Marshall 1994). Few Sphaeroceridae are likely to be confined to sedge meadows; many are associated with a range of decaying organic matter. Examples of such gen-

eralists collected in our study include *Loxophila atra* (Meigen), *Pullimosina pullula*, *Rachispoda* n. sp. 1, *Spelobia clunipes* (Meigen) and *S. luteilabris* (Rondani).

Many Ephydriidae are grazers of microorganisms and detritus in a range of wet habitats including mud shores, sedge meadows and beaches (Foote 1995). Our study sites were a combination of these three types of habitats. Nine of the species collected in our study were also recorded from peatlands by Blades and Marshall (1994) and eight from a freshwater marsh by Todd and Foote (1987b). *Notiphila caudata*, dominant in LAC sites, is abundant in a range of habitats including *Carex* meadows with exposed mud, marshes, beach wrack, mud shores and peatlands (Eastin and Foote 1971, Blades and Marshall 1994).

Species of *Plunomia* are associated with wetlands and *P. elegans* was the dominant species in all sites. Adults were reared from larvae or puparia found between the leaves of *C. lacustris* where the larvae probably feed on aphids such as *Thripsaphis* sp. (Drepanosiphidae) (Beaulieu and Wheeler 2002).

Diversity and abundance of trophic groups.—Over half of all specimens and over one third of all species identified were saprophagous. Predators were more species-rich but not as abundant. All other trophic groups ranked far behind in both species and specimens. This relative ranking was expected, given the nature of the study sites. Wetlands provide ample food sources for saprophagous larvae and such families are usually dominant (Blades and Marshall 1994 [reanalyzed for Brachycera only], Keiper et al. 2002). The low plant diversity at our sites may explain the less diverse phytophagous guild.

The lower diversity of saprophagous species in AQU1, particularly those in the substrate, is probably related to differences in substrate structure. The extensive wet mud in LAC sites may be a better habitat for detritivores and microbial grazers (e.g., ephydriids, sphaerocerids, some syrphids)

than the hummocky firm substrate in AQU1. The lower diversity of phytophagous species in LAC2 may be partly explained by the more heterogeneous vegetation in AQU1 and partly by the lower density of *C. lacustris* in LAC2. Despite the above differences, the similarity in trophic structure of Brachycera emphasizes the similarity of our study sites; they each consist basically of wet mud dominated by a single species of *Carex*. Given that we collected over 300 species of Brachycera in a single season, in three such “homogeneous” sites, Diptera diversity may be higher than expected even in apparently uniform habitats.

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